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The Number of Pilchards in the Channel

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I. INTRODUCTION

THE pilchard fishery off the Cornish coasts in the autumn yields between three and five thousand tons annually, a level of catch which has persisted for at least two hundred years. Measurements of length, age, and l_1 combined with vertebral counts have shown that the pilchards of Cornwall are probably the same fish as the 'célans' of Boulogne and the 'sardines' of Brittany (Le Gall, 1928; Furnestin, 1945). Consequently, it is likely that the Cornish pilchards really extend over a wide area—from the Straits of Dover to the edge of the continental shelf between Ireland and Brittany. From 1947-9, observations made by the yacht *Manihine* showed that pilchard eggs were to be found over extensive areas of the Channel in summer (Corbin, 1950). Linking these facts together, it seemed possible that the stock of pilchards was larger than appeared from the size of the fishery.

A reconnaissance cruise was made in June 1949 covering the whole of the Channel and it was found that pilchard eggs and pilchards were present all over the area, although more abundant in the West. This was followed by five cruises during the summer of 1950.

II. MATERIAL

PILCHARD eggs, larvae, plankton samples and temperature observations were collected at each station. The plankton samples were treated in the usual ways, but before the pilchard eggs and larvae were counted, developmental stages had to be devised.

From samples of pilchard eggs taken in the Channel during June 1949 (Cruise XI, *Sir Lancelot*, 1949), the development of the egg from spawning to hatching was split into twenty morphological stages; these were grouped into five main stages for convenience. The morphological stages, with their diagnoses and the groups of main stages are given in Table I.

Table I: *Developmental stages of pilchard eggs*

Morphological stage	*Diagnosis*	*Main stage*
1	Unfertilized.	
2	Fertilized: first cleavage stages appear.	
3	Formation of the blastoderm cap.	
4	Forward invasion by the blastoderm cap.	I
5	Invagination moves backward.	
6	Blastopore area becomes defined.	
7	*Embryonic shield appears from the blastopore area.*	

Table I: *Developmental stages of pilchard eggs—contd.*

Morphological stage	*Diagnosis*	*Main stage*
8	Appearance of neural crest and neural tube.	II
9	The embryo becomes built up from the egg surface from half to two thirds of the way round the egg.	
10	Appearance of the head.	
11	*Appearance of the optic vesicles.*	
12	Appearance of myotomes in the centre of the dorsal surface.	III
13	Myotomes appear in the head region and in the caudal region.	
14	Chromatophores appear and the embryo extends two thirds of the way round the egg.	
15	Eyes appear.	
16	*Appearance of the fin fold and the tail grows just clear of the egg.*	
17	Chromatophores extend to the end of the tail. The tail bends ventrally at one quarter of the embryo's length from the egg.	IV
18	*Anus appears; the back straightens and the tail bends ventrally at one half of the embryo's length from the egg.*	
19	Myotomes appear beyond the anus; the fin fold has grown to twice the width of the embryo.	V
20	*Hatching.*	

The developmental stages are illustrated in Fig. (1).

From the Helgoland larva net hauls, all the pilchard eggs were counted and classified into one of the main developmental stages.

III. METHODS

On Cruise XI, June 1949, it was found firstly that pilchard eggs were to be found from one end of the Channel to the other; and secondly that echo traces, presumably of pilchards, were similarly distributed.

From Hickling's (1945) study of the times of maturity of Cornish pilchards showing a peak of spawning in June, it seemed probable that most of the spawning period would be covered in a series of surveys from April to August inclusive.

In the summer of 1950, five 12 day cruises were carried out from April to August;

Cruise VII, *Sir Lancelot* 1950
Cruise VIII, ,, ,,
Cruise X, ,, ,,
Cruise XII, ,, ,,
Cruise XIV, ,, ,,

Stations were worked at fixed positions (see Fig. 2) on a grid that covered part of the Southern Bight from Lowestoft to Dover and the whole of the Channel from Dover to a line between Ushant and the Scilly Isles. On two cruises (Cruise VII and Cruise XII) we failed to complete the two western-most lines because of bad weather; on Cruise VII a survey was carried out in the region of the Channel Islands, which was never repeated because of disturbance to the Decca navigator in this region; on Cruise XIV a hydrographic survey was made to the west of Ushant.

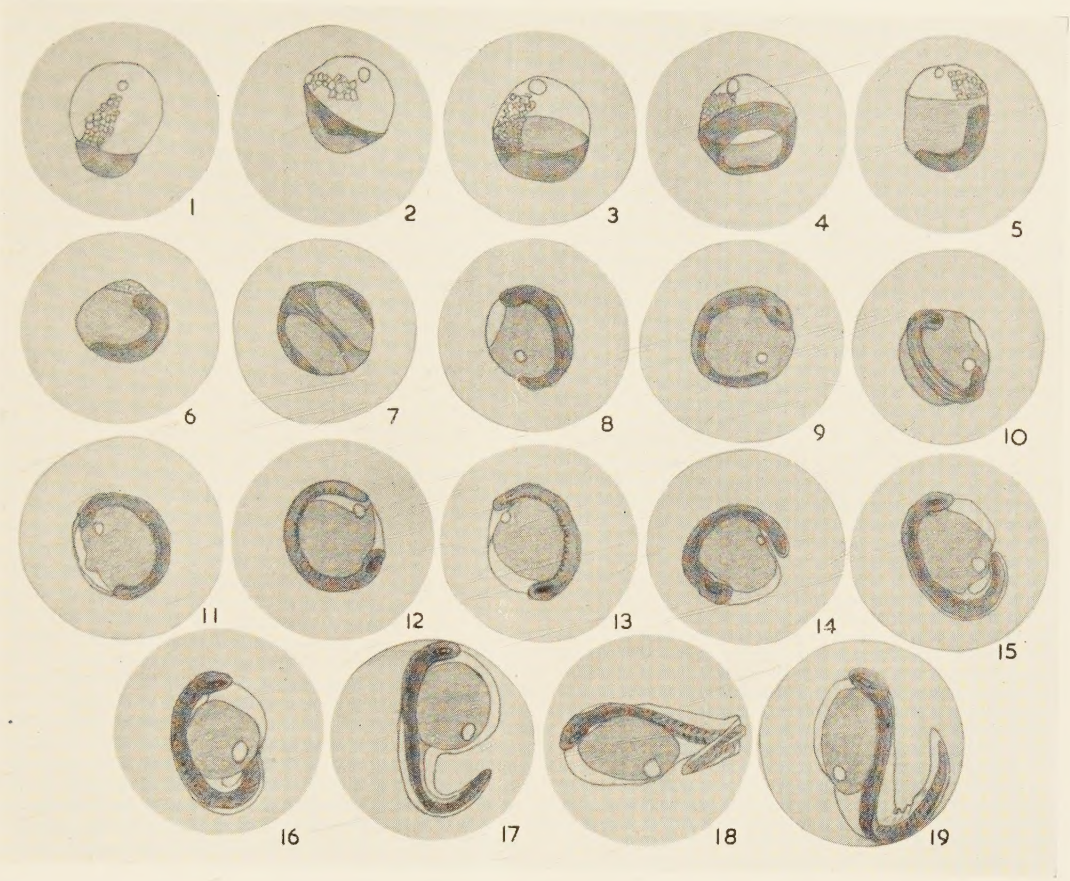

Fig. 1. *Developmental stages of pilchard eggs*

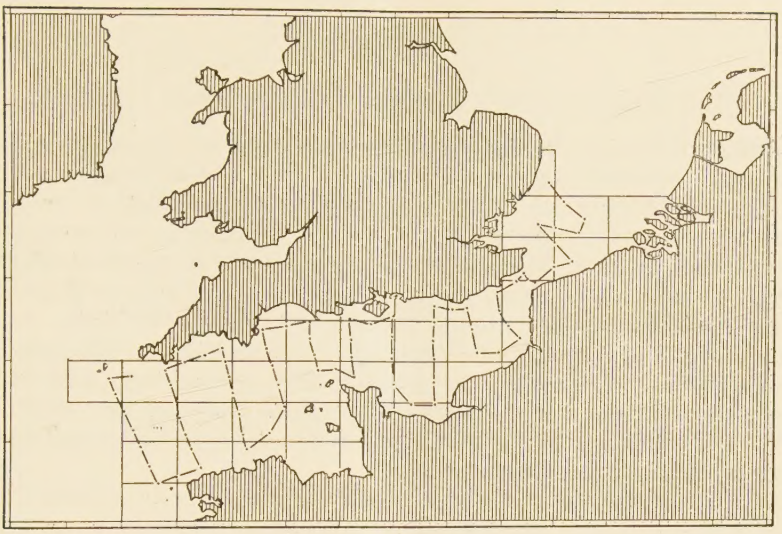

Fig. 2. *Station positions,* (— · —) *cruise track and statistical rectangles used on Cruises VII, VIII, X, XII and XIV* Sir Lancelot 1950.

At each station the following routine observations were made:

1. A Helgoland larva net, with a flowmeter in its mouth, was hauled from two fathoms off the bottom to the surface, with the use of the counterweight system (Buchanan-Wollaston, 1914). In order to maintain the correct hauling speed (1 m/2-3 sec) in the deeper water west of Plymouth, more weight had to be added to the counterweight. At depths greater than these (60 fms +), the counterweight method is of little use because the weight added to counter the weight of rope on the net side causes the net to accelerate as it comes up, for the weight of rope is being transferred to the counterweight side of the system.
2. Surface temperatures were read from the thermometer in a surface sampler, which had been shot away a few minutes before the station had been reached.
3. Water samples of 50 ml each from the surface samples were taken and preserved with the addition of a few drops of formalin. These were later examined by the sedimentation method for phytoplankton and counted.

The station routine was kept as short as possible, i.e., to the time of hauling of one Helgoland larva net, because the distances covered on each cruise were at the limit of the ship's range; even so, there was insufficient margin left for bad weather.

In the laboratory, pilchard eggs and larvae were separated out from the plankton; the pilchard eggs were separated into the five main stages and counted, results being tabulated as numbers /m^2 of each stage at each station. Larvae were separated out and a subsample was identified, using Lebour's method. Counts of each stage of pilchard larvae were made from Cruise XI 1949, Cruise VII 1950 and Cruise VIII 1950; subsequent counts were discontinued when it was realised that fish larvae escaped capture in daytime (Bridger, 1956). The information is used, however, to show the presence or absence of larvae in the crucial months of April, May and June.

Phytoplankton was counted by the sedimentation technique and tabulated as numbers of each species per litre at each station. Only limited conclusions may be drawn from the distribution of surface phytoplankton, as opposed to total phytoplankton, but some qualitative conclusions about its distribution in relation to the distribution of the pilchards are valid.

Zooplankton was counted by the whirling flask and Stempel pipette technique and expressed as numbers of each species per m^3 and as numbers of each species beneath m^2. This was because we were interested not only in the total quantity of zooplankton, but also in its effect as an aggregating factor for the pilchard.

IV. RESULTS

1. The Distribution of Pilchards in the Channel

The Cornish fishery for pilchards lasts from May to December ; from May to July the fish are present in small quantities only, the main fishery developing in October and November. At the same time in October and November there is a small fishery for pilchards off Boulogne and they are also caught in trammel nets in Rye Bay at this season. There are fisheries for sardines (immature pilchards 12-17 cm in length) all round the Brittany coast.

Russell (1935 *et seq.*) has reported the presence of pilchard eggs in large numbers in fortnightly ring trawl hauls at International Station E.1. Aurich (1953) has shown that in October pilchard eggs and larvae have occurred in large numbers in the Helgoland Bight particularly since 1949. On Cruise XVI *Sir Lancelot* 1951, pilchard eggs were found widely spread in fairly low numbers from Whitby to Helgoland and from the North Dogger to Smith's Knoll. In November 1951 pilchards occurred in large enough numbers in the East Anglian fishery to fill the drifters for a week.

Thus, there are two or three fisheries at widely separated points in the Channel that have been in existence for a very long time. Since 1935 there is some evidence of an increase in numbers of pilchard eggs at E.1 and there is some evidence of an extension of range northward into the Central North Sea. The latter points may be associated with the fact that the time of abundance of pilchard eggs at E.1 in 1913 to 1919 was from July to November and not from May to August as it is today (Clark, 1914; Allen, 1916; Clark, 1919); again Fage (1920) writes that the time of spawning at Arcachon and Concarneau was in May and June, whereas that in the Channel was in July and August.

Furnestin (1945), from a large quantity of measurements, distinguishes between a race of sardines living in the Gulf of Gascony and the race living in the Channel and round the Brittany coast (V.S. 51·76 for the 'Race Cantabrique' and V.S. 52·00 + for the 'Race Celtique'). Corbin (1947) has shown that in 1938 and 1939 the westward boundary of the distribution of pilchard eggs lay about 50-100 miles to the west of Ushant. At the time of planning the cruises in 1950, it was impossible to go far west of Ushant.

The chief problem is whether in charting the Channel from Lowestoft to Ushant, the major part of the pilchard stock was sampled; in other words, was the western boundary of the grid correctly chosen ? The adult fish are found in no fishery west or south of Cornwall; their migratory range appears to lie between the Celtic Sea and the Dogger. They are, however, frequently recorded on the southern and western coats of Ireland (Went, 1946).

The error due to the area sampled being less than the whole spawning area is unknown; as the edge of the spawning area in April 1938 (Corbin, 1947) was not more than one hundred miles west of Ushant and as the fish appeared to move up Channel in April, May and June, it is not thought that the stock is greatly underestimated.

Fig. 3 shows the distribution of stage 1 pilchard eggs and echo traces (expressed as the number of soundings on fish between stations) in June, 1949. There is a fair correlation between the two variables, enough to make us believe that echo traces in the Channel are most commonly due to pilchards. As populations of other pelagic fish, particularly horse mackerel, occur in the Channel, the correlation, if extended to individual traces or even to small regions, might very well break down. If, however, we confine our conclusions to comparatively large regions (e.g., one quarter or one third of the Channel) we can assume that most echo traces are due to pilchards. In other areas, fish traces are found perhaps only at night or only in the daytime; when this is so, echo surveys are of no use to estimate abundance. A test of the possibility of the diurnal appearance of echo traces was made by grouping the numbers of soundings on fish in two-hourly intervals, e.g., 2400-0200 hr, 0200-0400 hr, etc.; the results are shown in Table II, grouped by cruises.

From Table II it will be seen that there is a pronounced rise in the mean number of soundings on fish from dawn till 1000 hr, but it is thought that this is primarily due to a limited area of high soundings being found between dawn and 1000 hr on one day of Cruise VII. There is a similar but less pronounced trend to be found on Cruise VIII and

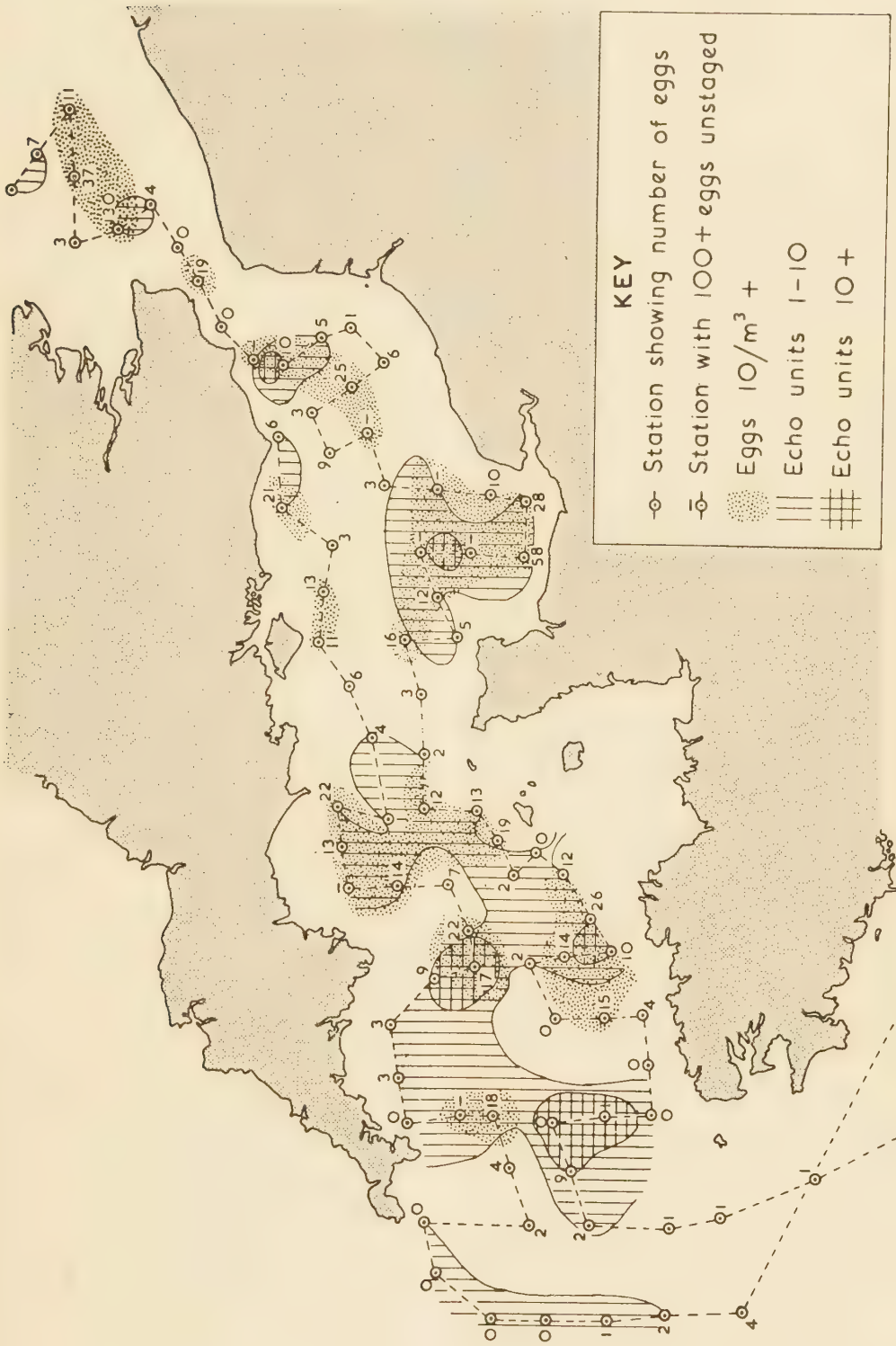

Fig. 3. *Distributions of Stage I pilchard eggs and echo traces of fish on Cruise XI*, Sir Lancelot 1949.

Table II: *Mean numbers of soundings on fish at different times of day, Cruises VII, VIII and X*, Sir Lancelot, 1950

The number of echograms used to contribute to each mean is shown as a suffix.

Time of day	24–02	02–04	04–06	06–08	08–10	10–12	12–14	14–16	16–18	18–20	20–22	22–24
Cruise VII	66_2	55_3	163_3	254_2	135_4	119_2	42_3	46_4	19_3	53_3	22_3	8_3
VIII	14_2	40_3	33_5	63_4	87_4	167_1	31_5	77_4	83_4	10_5	137_3	12_1
X	60_2	58_6	43_6	29_4	70_5	38_4	41_3	37_3	28_4	18_4	37_3	97_1
Mean	46·7	52·7	65·1	87·6	95·2	79·6	36·7	54·8	45·5	23·4	65·3	26·6

none on Cruise X. One might expect that traces were found more by night because the shoals go deep in daytime, or more by day because they disperse at night but the numbers were not very different; about 4,000 soundings on fish were made in daylight as compared with 3,000 soundings on fish at night during the three cruises. The differences considered in using the results are much greater than that.

Fig. 4 shows the distribution of echo traces in Cruises VII, VIII, X, XII and XIV, *Sir Lancelot*, 1950. In April (Cruise VII) the echo traces are found in a patch between Start Point and the Channel Islands. The western boundary of the patch was not defined because the two western-most lines of stations were not completed; the eastern boundary of the main patch lay between Portland and Cap Barfleur. No traces at all were found east

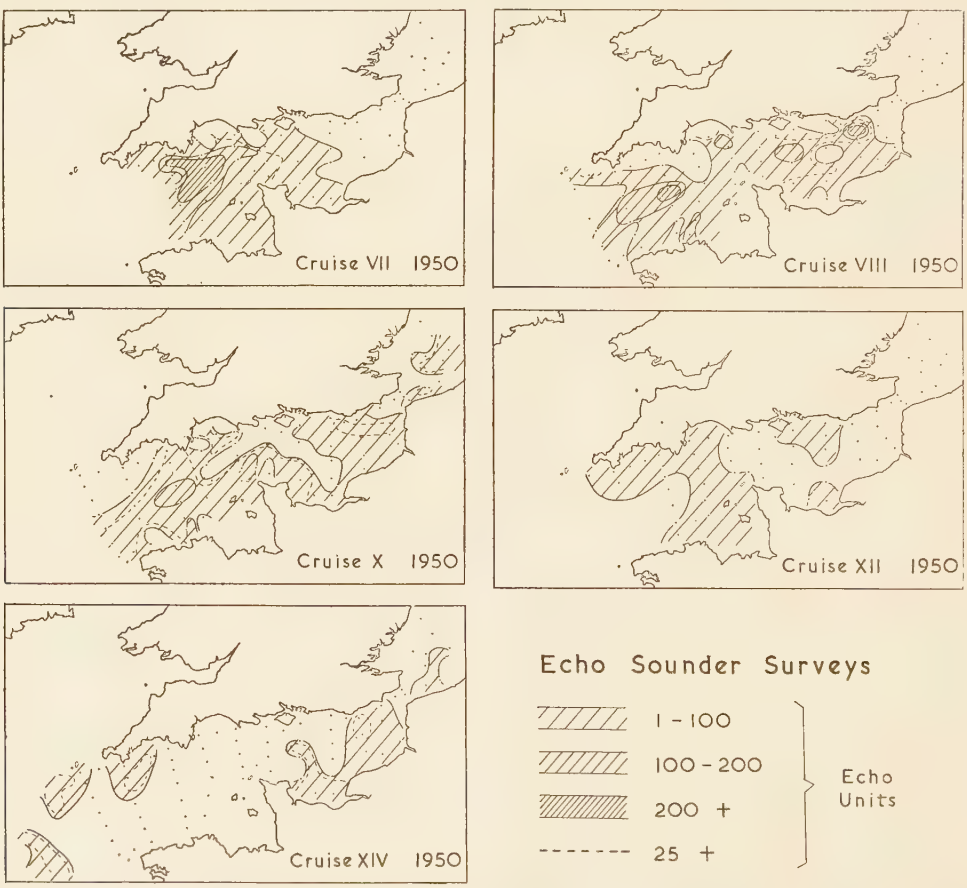

Fig. 4. *Echo surveys of the Channel, Cruises VII, VIII, X, XII and XIV*, Sir Lancelot 1950

Echo units are expressed as 'per unit distance'.

of a line between Beachy Head and Cap d'Antifer. It was on Cruise VII that certain stations were made within the Channel Islands region, but few fish traces were observed there.

In May (Cruise VIII), there were five patches, each of them quite small; the largest lay between Cornwall and Brittany right in the middle of the Channel. Since the April cruise a general easterly movement has taken place; the eastern boundary lies between Hastings and Fécamp and fairly thick traces have moved east from Start Point to the Cherbourg-Isle of Wight line and even to Beachy Head. In view of this easterly movement it is perhaps significant that few traces were observed on the western-most line from Ushant to the Scilly Isles. No fish traces were observed in the region within five miles of the Lizard to within ten to fifteen miles of the Start Point.

In June (Cruise X) fish traces were observed as far east as the Central Southern Bight of the North Sea. No dense patches of echo trace were seen, most being fairly uniformly distributed over quite a wide area. Most fish traces were found in the western half of the Channel, although there was a barren stretch in the central region and another in the extreme west.

In July (Cruise XII) fish traces were found at a comparatively low level of density between Start Point and the Channel Islands and between Beachy Head and the Baie de la Seine.

In August (Cruise XIV) few traces were observed, in two regions—a few in the extreme west and some in the region between the Baie de la Seine and the Southern Bight.

There are two conclusions from these distributions, firstly, that between April and June an easterly movement of fish took place and secondly that in June and July the echo traces disappeared. There are two possibilities to account for this disappearance; either the fish have moved east so far as to leave the region being sampled, or that after the peak of spawning in June, they disperse out of reach of the echo sounder. By this I mean that they could be widely scattered in the midwater, drifted far inshore or lying very close to the bottom.

Fig. 5 shows the distribution of pilchard eggs expressed as numbers /m² on Cruises VII, VIII, X and XII *Sir Lancelot* 1950. Cruise XIV has been omitted because there was only one station of more than 100 eggs/m². These distributions are perhaps less reliable than the echo surveys for showing the whereabouts of all the fish, but they are more reliable for

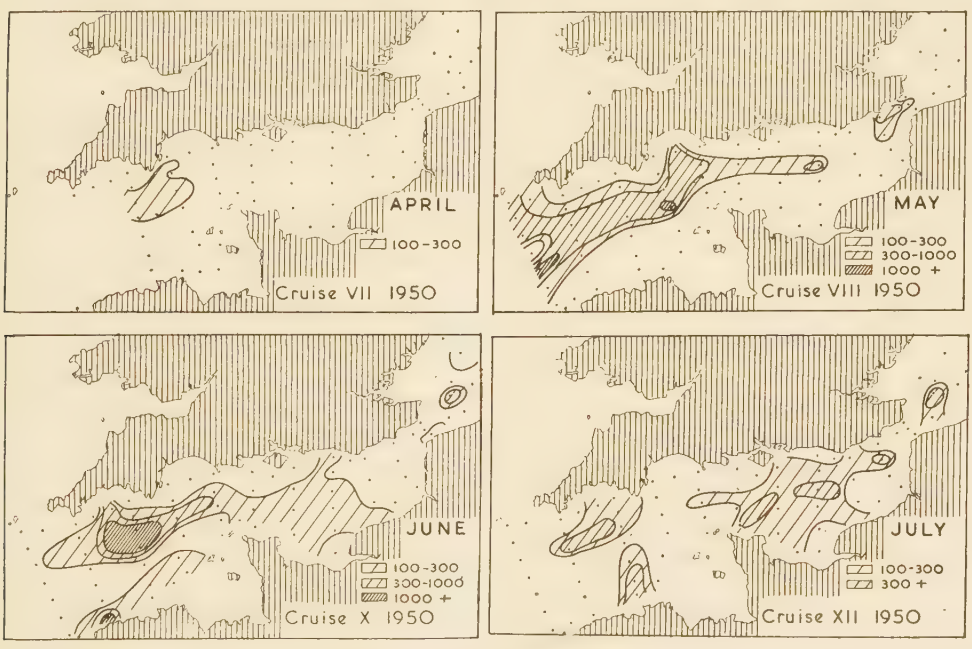

Fig. 5. *Distributions of pilchard eggs as numbers beneath m² on Cruises VII, VIII, X and XII* Sir Lancelot 1950.

showing where the spawning fish were most abundant. Most striking is the eastward extension of spawning between April and May, which from the echo survey distribution is probably an eastward movement. Also remarkable is the tendency of fish to spawn in the centre of the western half of the Channel. Another point is that in June, the month of peak spawning, the line between Ushant and the Scillies seems to form the western boundary to the numbers of eggs; this was also so in June 1949.

Combining the results from echo survey and those from the egg distributions, it seems possible that the fish are in the Western Channel in April, that they extend eastwards during May and June and that although some may reach the Central North Sea, the main body of the population remains in the Western Channel, i.e., from the Ushant-Scillies line to the Portland-Cap Barfleur line.

In July, spawning is equally spread over all the Channel at a fairly low level. The full effect of movement can be shown by comparing the egg charts for April and July, which are comparable in magnitude. The fish migrating furthest may spawn a little later than the more abundant fish remaining in the Western Channel, or the eastern migrants may be recovering spents from the west. As the fish appear both on the Cornish coats and off Boulogne in October, it seems likely that the Western Channel fish gradually gather in inshore Cornish waters in the autumn and that the eastern migrants gradually fall back from the Southern Bight towards Boulogne in autumn and to the Western Channel in winter.

An extension of this pattern of migration is that the fish withdraw westwards into deeper water in the dead of winter, reappearing off the Wolf at the end of March and up-Channel towards Start Point in April. If this is so it is reasonable to believe that the stock is a single one mixing with its southern neighbours in the Gulf of Gascony rarely, because it is divided from them by its time of spawning. It will be assumed that the majority of the population was adequately sampled by the cruises undertaken.

2. The Vertical Distribution of Pilchards

As each echo trace was measured in width, so also was its depth recorded. The depth was the minimum depth recorded on the echogram; no further information was noted because of the possibility of multiple reverberation between fish. The minimum depth recorded in this way is not a true depth, but is nearly always an overestimate because the echo sounder reports signals in midwater not from the indicated depth, but from an indicated range, which may be a slight angular range.

The indicated depths of echo traces were grouped in two hourly intervals from midnight to midnight for each cruise. The results are shown graphically in Fig. 6. A very marked vertical migration is shown, ranging from 12 fms just before midnight to 25-28 fms at midday. On Cruise VII, in April, the amplitude of the migration was from 7-28 fms, whereas on Cruise VIII it deepened to 12-27 fms; on Cruise X the migration appears to be of a different character, extending from 10-25 fms. It is possible that the difference between Cruise VII and VIII is a function of longer day and slightly stronger light at midday, but the difference between the migration on these cruises and that in Cruise X cannot be related to differences in light, but is perhaps related to the completion of spawning.

Ahlstrom (1943) found that the Californian pilchard, *Sardinops caerulea* lays its eggs in the upper 30m of the sea just before midnight. It was thought that the English pilchard might behave in a similar way. At a few stations, the Helgoland larva net was hauled to the surface from a number of different depths to find the vertical distribution of eggs. Table III gives the results of these hauls as numbers/m^2 (from the depth hauled) of Stage I pilchard eggs. As this development stage may last a day or more, there is plenty of time for the eggs to be swirled away from the surface. Table III shows that on station 60, Cruise VII, some eggs were found in the top fifteen fathoms; on Cruises VIII and X, a minority were found in the top layers. As these sets of hauls were all taken at night, no evidence is shown that eggs were laid at night when the fish had migrated to the upper layers; it is possible, however, that the duration of the developmental stage I is long enough to cause confusion—in which case the eggs must sink, which seems unlikely. The simplest explanation is that most of the eggs are laid at midday.

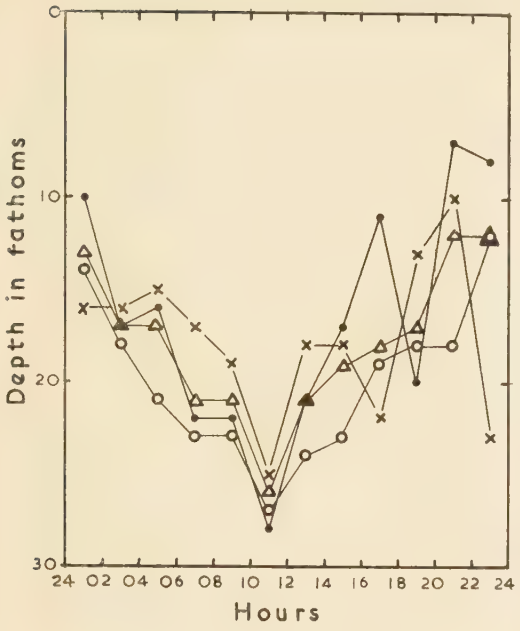

Fig. 6. *The diurnal distributions of echo traces on each cruise*

- Cruise VII, *Sir Lancelot*, 1950
- „ VIII „ „
- „ X „ „
- mean

Table III: *Vertical distribution of Stage I pilchard eggs*

Cruise and Station Depth and No.	VII. 60		VIII. 61		VIII. 84		X. 11		X. 33		X. 57		X. 61		X. 64	
	fms	no.	fms	no.	fms	no.	fms	no.	fms	no.	fms	no.	fms	no.	fms	no.
	36	187	32	137	30	216	20	87	32	96	38	50	36	1174	32	353
	25	118	20	132	20	32	15	50	20	85	26	49	26	544	22	437
	20	143	10	43	10	29	10	20	10	50	16	27	16	279	12	164
	15	191	5	51	–	–	5	14	5	32	6	–	6	56	5	110
	10	100	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	5	56	–	–	–	–	–	–	–	–	–	–	–	–	–	–

3. Estimation of the Numbers of Adult Pilchards in the Channel

The region was split into a number of rectangles, each of which contained three, four or five stations. The distribution of the rectangles and the fixed stations are shown in Fig. 2. The area of each rectangle was measured on the chart in Km^2.

The total number of pilchard eggs of all stages is expressed as the number/m^2 at each

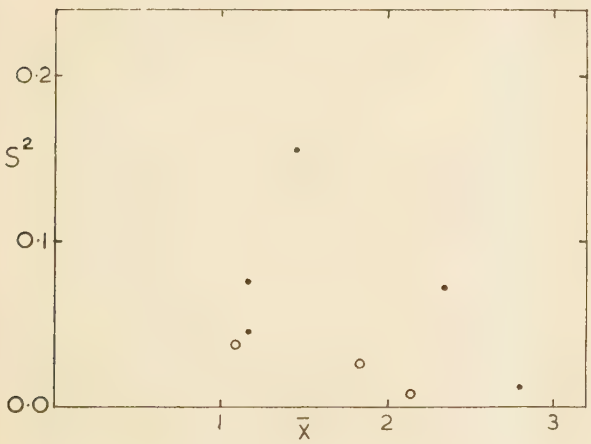

Fig. 7. *Relation between variance and mean of replicated hauls of Hensen net* (●) *and Helgoland larva net* (○) *for different developmental stages of pilchard eggs.*

station. An average number/m² is then derived for each rectangle and weighted for the area of the rectangle.

On Cruise XII, off Cherbourg, a series of twenty hauls were made with a Hensen net and a Helgoland larva net alternately. The catches of pilchard eggs in each net were counted, and grouped into developmental stages. Expressed as numbers/m², the numbers of eggs of each stage and each net for each haul were transformed by log $(n + 1)$; means and variances of the transformed numbers were obtained. Fig. 7 shows variance plotted against mean and the lack of regression justifies the use of the simple transformation for making estimates of the variance of numbers.

In order to obtain an estimate of the error of the average number of eggs/m² per rectangle, the following analysis of variance on transformed values was undertaken.

Table IV: *Analysis of variance of the average number of eggs/m² within and between rectangles*

	VII		VIII		X		XII		XIV	
	DF	M. Sq.	DF	M. Sq.	DF	M. Sq.	DF	M. Sq.	DF	M. Sq.
Within rectangles	15	0·510	36	1·310	44	0·679	38	0·569	16	0·612
Between rectangles	6	1·639	21	1·431	28	1·006	23	1·023	8	0·343
Total	21	0·833	57	1·355	72	0·806	61	0·740	24	0·522
$\sqrt{\text{Within rectangles}}$	0·714		1·145		0·824		0·754		0·782	
Antilog − 1	4·177		12·95		5·668		4·679		5·053	
S^2	17·45		167·7		32·13		21·89		25·53	

Let m be the average number of eggs/m² per rectangle, A be the area of the rectangle, then $m \cdot A$ is the estimated number of eggs in each rectangle and $\sum(m \cdot A)$ is the estimated number of eggs per cruise.

Let S^2 be the 'within rectangles' mean square (from Table IV).

Let K be the number of stations in any given rectangle,

then the variance of the number of eggs per cruise is given by

$$\sum\left(m^2 \cdot A^2 \cdot \frac{S^2}{K}\right).$$

Before the total number of eggs produced during the year in the region sampled can be estimated, a measure of the effect of temperature on the development of pilchard eggs must be obtained. For this purpose, an artificial fertilization was made at sea off Newlyn on 16th June, 1953 and the fertilized eggs were taken to Plymouth in thermos flasks at the sea temperature.

In the laboratory at Plymouth (with the kind permission of Mr. F. S. Russell, F.R.S.) batches of eggs were kept at constant temperatures of 5°C, 14°C and 17°C until hatching. At intervals the eggs were examined and the numbers in different developmental stages were noted. The main result was that at 14°C development from fertilization to hatching took 78 hours and that at 17°C it took 57 hours; the eggs kept at 5°C never survived beyond stage I.4.

Fig. 8 shows the relation between time in hours and the average developmental stage reached by that time. From the character of the relation shown, it appears that the later more complex stages of development take progressively longer. As time of development to hatching is in general inversely proportional to temperature (Belehradek, 1935), a line was drawn through the two observed points as shown in Fig. 9. With the use of this line, the

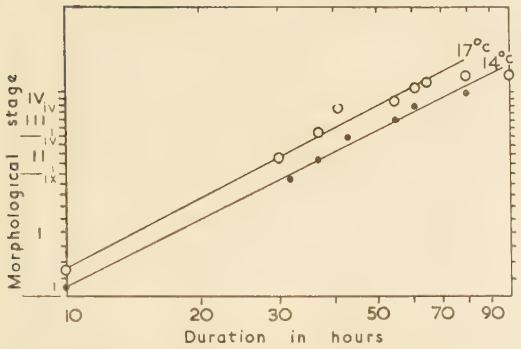

Fig. 8. *Duration of developmental stages at 14°C and 17°C.*

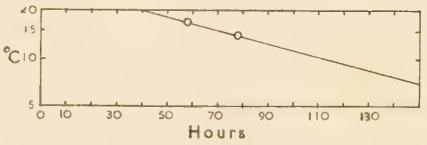

Fig. 9. *Relation between temperature and the duration of hatching period.*

duration in hours of development was read off for different regions and seasons in the Channel.

Charts of surface temperature were drawn up for each cruise by my colleague, Mr. D. Vaux, and from these charts average temperatures for each rectangle on each cruise were calculated. Hence it was possible to read off developmental times in hours for each rectangle on each cruise.

The period between the beginning of Cruise VII and the end of Cruise XIV was divided up into equivalent parts, so that, for example, the samples from Cruise VII represented thirty days. The developmental time in days was divided into this 'representative cruise period' to give a temperature factor Q. The total number of eggs produced in each 'representative cruise period' is then given by the product $\sum(m \,.\, A \,.\, Q)$. Such values were worked out for each cruise and were multiplied by the unit of area used, A, where $A = 3.92.10^7 m^2$, to give estimated numbers of eggs produced in the whole Channel for the 'representative cruise period'; added together for all 'representative cruise periods', the sum is an estimate of the total number of eggs produced in the Channel.

The steps in this calculation are set out in Table V, which includes estimates of error derived from values of

$$\sqrt{\sum\left(M^2 \,.\, A^2 \,.\, \frac{S^2}{K}\right)}.$$

It will be noticed that such estimates are also multiplied by $\bar{Q}$, by A and added for all 'representative cruise periods' to give an estimate of error. $\bar{Q}$ is an average estimate of Q

Table V: *Estimation of the number of pilchard eggs in the Channel in* 1950

Cruise	*'Representative Cruise Period'* (days)	$\Sigma(M.A.Q)$	$\Sigma(M \,.\, A \,.\, Q) \times 3{\cdot}92 \times 10^7$	$\sqrt{\Sigma\left(M^2 \,.\, A^2 \,.\, \frac{S^2}{K}\right)}$	$\bar{Q}$	$\bar{Q}\sqrt{\Sigma\left(M^2 \,.\, A^2 \,.\, \frac{S^2}{K}\right)} \times 3{\cdot}92 \times 10^7$	
VII	(30)	220,883	$8{\cdot}65 \times 10^{12}$	65,503	6·24	408,739	$16{\cdot}00 \times 10^{12}$
VIII	(32)	2,941,936	$115{\cdot}18 \times 10^{12}$	1,107,585	7·35	8,140,750	$318{\cdot}71 \times 10^{12}$
X	(33)	4,886,852	$191{\cdot}32 \times 10^{12}$	904,833	9·98	9,030,233	$353{\cdot}53 \times 10^{12}$
XII	(29)	2,136,956	$83{\cdot}66 \times 10^{12}$	174,289	10·40	1,812,606	$70{\cdot}96 \times 10^{12}$
XIV	(30)	164,449	$6{\cdot}44 \times 10^{12}$	26,880	12·57	337,882	$13{\cdot}23 \times 10^{12}$
Total			$405{\cdot}3 \times 10^{12}$				$481{\cdot}7 \times 10^{12}$

for each cruise, used in computing the variance. As this estimate of error is really a log normal one, it is best represented as a factor, i.e., in this case, as: $\times$ 2·2, $\times$ 0·45.

In order to calculate the number of adult females in the Channel, an estimate of the fecundity of the pilchard is necessary. Before the work of Andreu (1954) there was only observation of the number of eggs in each female —60,000 (Cunningham, 1893). Hickling and Rutenberg (1936) considered that the pilchard spawned continuously during an extended season and that there was no sharp distinction between ripening ova and the general stock of ovocytes. Andreu (1951), using a histological scale of maturity and by measuring a large number of ovarian eggs was able to distinguish (a) planktonic eggs, 1500μ in diameter, (b) ripe eggs, 1000μ in diameter, (c) first ripening stock, 650μ in diameter, (d) second ripening stock, 350μ in diameter and (e) ovocytes, 80μ in diameter (Andreu, 1954). From Andreu's measurements, it appears that the pilchard (or Atlantic sardine) may spawn perhaps twice in the same season; but it is also clear that an estimate of fecundity is possible if all eggs larger than 200μ in diameter are counted. Andreu (1954) gives the length/fecundity relation for a sample of 46 fish ranging from 12 to 21·5 cm in length.

From Hodgson and Richardson (1949) a mean length of mature pilchards of 20·5 cm was taken; from Andreu's data such fish would have a fecundity of 76,000 eggs. Using this figure, the number of adult female pilchards in the Channel becomes $(405{\cdot}3 \times 10^{12}/76000) = 5{\cdot}33 \times 10^{9}$. Assuming for our present rough purposes that the sex ratio is unity, the population of mature pilchards in the Channel is $10^{10}(\times 2{\cdot}2, \times 0{\cdot}45)$.*

4. The Number of Fish Recorded with each Transmission of the Echo Sounder

As the dual purpose of the Channel cruises was to estimate the number of pilchards living there and also to chart their horizontal distribution by counting the number of soundings on fish on each cruise, it becomes possible to estimate the number of fish contributing to each sounding on fish. Any estimate of this character is bound to be a very rough one, because of variances due to sampling, and to vagaries in acoustic measurements underwater. The method of survey used relies on the presence or absence of signal from fish in any one transmission, which is confirmed in the next and subsequent transmissions; although the signal-to-noise ratio obtainable in this way is high, it is hard to know whether it is being reproduced on another echo sounder. However, apart from the converse observations made on single fish (Trout, Lee, Richardson and Harden Jones, 1952) no estimate of the number of fish per sounding is available at all.

Table VI gives the total number of soundings on fish recorded on each cruise during the series:

Table VI: *Number of soundings on fish on each cruise*

Cruise	VII, April	2771
,,	VIII, May	2159
,,	X, June	1853
,,	XII, July	244
,,	XIV, August	896

In July and August there is a sharp decrease in the number of soundings on fish. This is due either to emigration or dispersion. By dispersion, I mean that the shoals break up into units that are in general too small for detection. So when spawning is complete the spent fish may scatter, swimming or drifting singly, beyond the sensitivity of the echo sounder. A similar phenomenon has been observed in the Southern Bight in January, February and March, when the spent herring drift back from the Straits of Dover: echo traces are observed, but they are much fewer in number than those seen during the East Anglian herring season when the fish are approaching the Straits.

It will be assumed that the numbers of soundings on fish in April, May and June are equivalent samples of the stock as counted from the egg samples. The average of the three

* From Andreu (1957) it appears from histological examination that a steady production of ovocytes may take place; so, more than one spawning could occur in a season. If this were so, perhaps the number arrived at should be halved; however, as the spawning period fits in with the fat cycle (Hickling, 1945) it is likely that the present method is valid as an estimate of fecundity.

estimates is 2261 soundings. An estimate of the number of fish per transmission is derived as follows:

The MS XII echo sounder made $44\frac{7}{9}$ transmissions/min at $10\frac{1}{2}$ knots, the *Sir Lancelot* covered 5·4 m/sec, which gives an interval of 7·2 m in distance steamed between transmissions.

The distance steamed on each cruise, d_s, is $2{\cdot}6 \times 10^6$m (from the station chart, Fig. 3).

The volume sampled in one sounding, V_s, is $V_s = \frac{1}{3}\pi r^2 . d$ where d is the average depth in the Channel, 72 m, and r is the radius of the base of the sound cone at 72 m (taking a half angle of 15°).

The total number of soundings, n_s, is d_s/m where m is the interval between soundings, 7·2 m.

The number of fish under the sounder, N, $= 10^{10} \times (V_s \times n_s/V)$, where V is the volume of the Channel (including part of the Southern Bight) $= 6{\cdot}7 \times 10^{12} m^3$.

So the number of fish per sounding is

$$\frac{N}{2261} = \frac{10^{10} \times (\frac{1}{3}\pi\, 19{\cdot}5^2 . 72) \times (7{\cdot}2 \times 2{\cdot}6 \times 10^6)}{2261 \times 7{\cdot}2 \times 6{\cdot}7 \times 10^{12}} = 6834.$$

The error on this estimate is contributed from two sources, firstly the error on the estimate of numbers of fish ($\times$ 2·2, $\times$ 0·45) and secondly on the unknown error attributable to the method of echo sounder sampling. Of the latter, it is possible that the error is less than might be imagined, partly because there is a range of ten times in the signal recorded on the paper and partly because the total numbers of echo traces recorded in April, May and June were all roughly comparable in magnitude. The consistency of the three estimates made before spawning was complete leads one to believe that the error might not be too high.

5. Relation of the Pilchard to its Environment

Three factors in the external environment of the pilchard were recorded during Cruises VII, VIII, X, XII, and XIV: temperature, phytoplankton and zooplankton. The plant and animal plankton have been separated because although the pilchard occasionally eats phytoplankton, it is much more likely to use zooplankton for its main food (Swithinbank and Bullen, 1913, 1914; Hickling, 1945).

(a) *The relation of spawning to temperature*

Temperatures were measured at each station by means of a thermometer in a Surface Sampler. These observations were averaged for each square and tabulated with the average number of eggs/m² in each square. Fig. 10 shows the average numbers of eggs/m² plotted against the average temperature in each square to the nearest half degree, Centigrade. It is a little difficult to decide whether this figure shows a normal distribution of frequencies of numbers of eggs, with a mean at about 13°C or whether it shows a lower limit to spawning at about 9°C and an upper limit to spawning at about 17°C.

To try to decide this question, the average number of eggs recorded at each half degree of temperature were set down at each level of temperature in half degrees between 8·5°C and 17·5°C in Table VII.

Table VII: *Average number of eggs/m² at each level of temperature*
Suffices are numbers of stations

Temp. (°C.)	8·5	9·0	9·5	10·0	10·5	11·0	11·5	12·0	12·5	13·0	13·5	14·0	14·5	15·0	15·5	16·0	16·5	17·0	17·5
Av. no. eggs	12_2	–	43_2	119_9	276_6	202_5	344_4	–	192_1	87_4	102_8	446_8	65_2	94_7	130_8	123_6	50_3	15_2	2_2

From 10°C to 16°C, there is no limiting effect, i.e., the numbers of eggs appear to be randomly distributed with respect to temperature. Above 16°C, the number of eggs dies

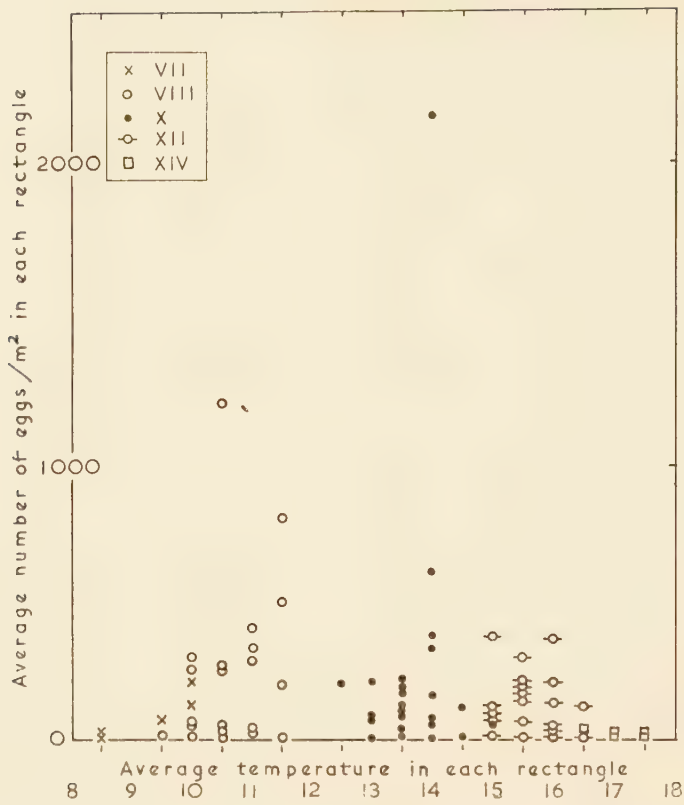

Fig. 10. *Relation between the average numbers of pilchard eggs in each rectangle on each cruise and the average temperature in the same rectangle.*

away but this is probably due to the end of spawning; Fig. 10 shows that there are only five observations on Cruise XIV, four of which were at 17·0°C and 17·5°C and all are low. Below 10°C it appears possible that temperature was having some effect, for on Cruise VII, the observations at 8·5°C were considerably lower than those at 10°C (8·5°C – 12 eggs and 10°C – 107 eggs). However, the spawning at 9·5°C – 10·0°C took place off Plymouth and off Start Point and the spawning at 8·5°C took place in the Pas de Calais. As echo traces were found in the West only, it may be that the apparent difference in spawning with temperature was really a difference due to numbers of adults, which in itself, however, could be an effect of temperature.

The relation between the echo traces, or adult fish, was obviously non-existent in detail when temperature distributions and echo-trace distributions were compared from cruise to cruise, but in April the distribution of eggs was bounded by the 9·5°C isotherm. We do not know when or how the fish retreat to the west, but it is quite possible that their eastward advance in late March and early April is related to temperature distributions.

(b) *The relation with phytoplankton*

Swithinbank and Bullen (1913) and Hickling (1945) have noted that phytoplankton organisms, diatoms, ceratia and *Phaeocystis* have been found in marked quantities in pilchard guts. It is possible that the fish take the plants willy nilly with the animals, because the mesh-size of the pilchard's gill rakers is very small; it is also possible that the fish feed on *Oikopleura* and consequently get phytoplankton in their guts; the last possibility is that pilchards feed on diatoms.

Phytoplankton samples were taken as water samples from the surface sampler; these were counted by the sedimentation technique, certain measurements of cells were made and from these with numbers of plants per litre, estimates of algal volume/litre in μ^3 were derived.

Algal volumes at each station were correlated with the numbers of soundings on fish between stations; for this purpose the number of soundings on fish at any given plankton station was taken as the mean of the two values taken approaching and leaving the station. Table VIII gives the correlation coefficients worked out for two groups of stations separately on Cruises VII, VIII and X; stations 1-41 included the area east of a line between Cap Barfleur and Weymouth and stations 42-82 included the area west of that line.

Table VIII: *Correlations of the number of soundings on fish on algal volumes per litre at the surface*

Cruise	*VII*	*VIII*	*X*
Stations			
1 – 41	– 0·1572	– 0·0135	+ 0·2331
42 – 82	– 0·3111	+ 0·5011*	+ 0·3913†

*Significant at 0·01 level.
†Significant at 0·05 level.

Table VIII shows a remarkable result that for stations 42 – 82 on Cruise VIII there was a distinct correlation between the fish recorded by the echo sounder and the quantity of algae at the surface. As the correlation coefficient is being used to measure aggregation of fish on to plankton, we may also note that the coefficients in April (Cruise VII) are negative and those in June (Cruise X) are positive; none of these are significant, but as measures of aggregation those for Cruise X are relatively high. This implies that the algal plankton was worth aggregating on in the Western Channel in May and that the effect persisted slightly in June over all the Channel.

Fig. 11 shows the distribution of algal volume at the surface in μ^3 per litre. It will be seen that there is no obvious spatial aggregation of fish upon algae in the Western Channel on Cruise VIII, but that there are three positions at which the distributions coincide—off Weymouth, in mid Channel, South of Start Point and off the North Brittany Coast; it is possible to identify these positions on the subsequent cruise, but on both cruises the general distributions, apart from these three positions, seem to be arranged independently.

The possibility that spawning was related to algal distributions was considered; Table IX shows the correlation of numbers of Stage I pilchard eggs on algal volumes.

Table IX: *Correlations of the number of stage I pilchard eggs/m² on algal volumes/litre at the surface*

Cruise	*VII*	*VIII*	*X*
Stations 42 – 82	– 0·3371	– 0·0941	– 0·0085
n	24	36	34

Hence spawning was not related to the quantity of phytoplankton. One is left with the possibility that the non-spawning fish aggregated on phytoplankton patches, whereas the spawning fish did not.

(c) *The relation with zooplankton*

The main conclusion from the work of Swithinbank and Bullen (1913, 1914) was that although pilchards feed on both phytoplankton and zooplankton, they take zooplankton

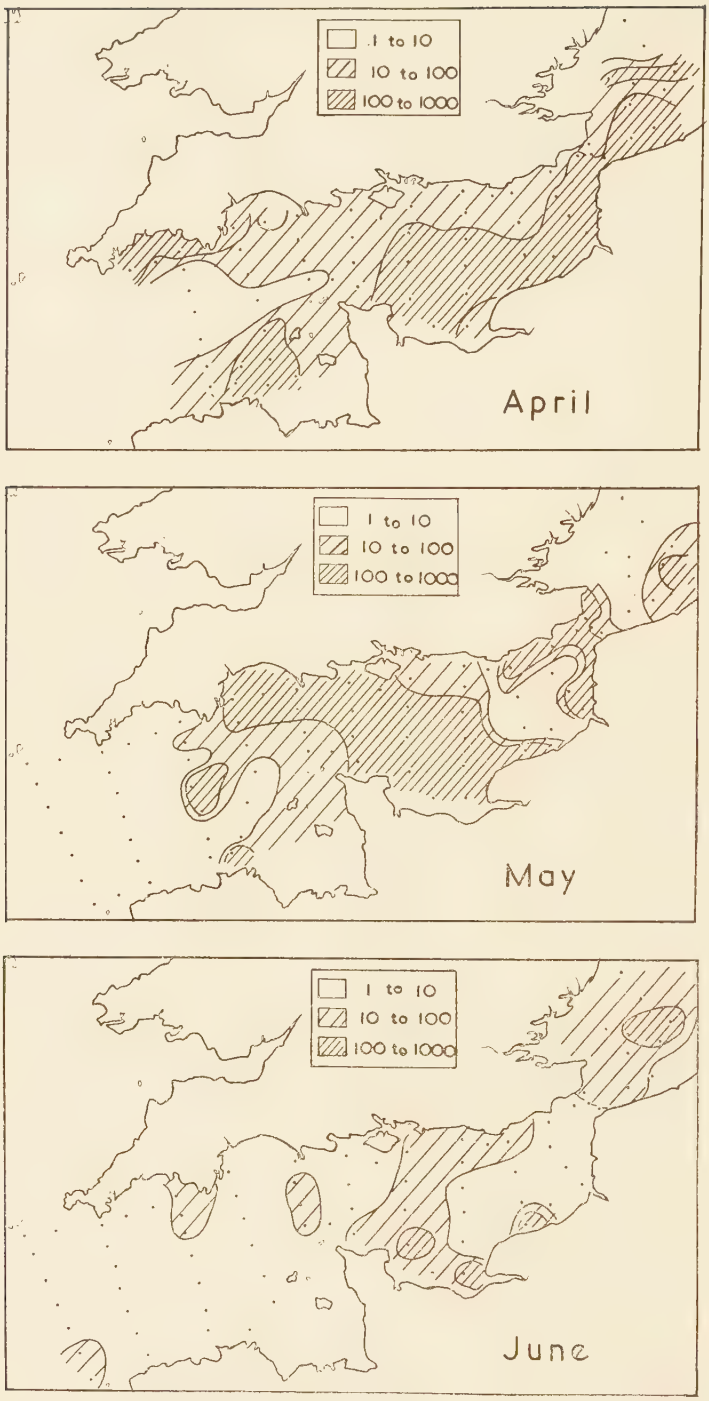

Fig. 11. *Distribution of algal volumes as* $\mu^3 . 10^8$*/litre, on Cruise VII, VIII and X,* Sir Lancelot, 1950. *Contours at* 10 *and* $100\mu^3 . 10^8$*/litre.*

in preference to the algae. As herring have been shown to aggregate actively on to patches of *Calanus* (Cushing, 1955) it was thought possible that pilchards might also aggregate on to patches of their food. One of the results of the work on *Calanus* was that a greater degree of aggregation was demonstrated on older stages of *Calanus* than on younger and that the degree of aggregation on non-calanid copepods was very small indeed.

A preliminary search for a food selected by the fish was made by plotting the numbers of soundings on fish at each station (in fact averaged between the inter-station distances before and after each station) against the numbers/m³ of various zooplankton organisms at each station. No evidence of correlation was observed on any of the graphs obtained in this way. It was decided to group the animals into size groups as follows:

I	II	III	IV
1 mm³	1 – 2·5 mm³	2·5 – 5 mm³	5 mm³
Calanus I *Paracalanus*	*Calanus II* *Paracalanus* *Pseudocalanus* *Acartia* *Centropages*	*Temora* *Pseudocalanus*	*Calanus III* *IV* *V* *VI*

This preliminary work was carried out for me by Dr. Ben-Tuvia.

At each station on each cruise, the numbers of each size group/m³ were added together irrespective of species. Correlations were estimated between these values and the numbers of soundings on fish averaged for each station as described above. The correlations were carried out for stations 1 – 41 and 42 – 82 on each of Cruises VII, VIII, X and XII; the Eastern Channel, east of a line between Portland and Cap Barfleur is covered by stations 1 – 41 and the Western Channel, west of that line, is covered by stations 42 – 82. The coefficients are given in Table X.

Table X: *Correlation coefficients between numbers of soundings on fish and numbers/m³ of zooplankton organisms, grouped by size*

Cruise		*VII*	*VIII*	*X*	*XII*
Stations 1 – 41	Size Group I	− 0·1794	− 0·1368	+ 0·2535	− 0·1042
	II	− 0·3115	+ 0·0110	+ 0·0565	+ 0·1713
	III	− 0·2742	− 0·1572	+ 0·0962	+ 0·3692
	IV	− 0·1613	+ 0·1086	+ 0·1537	+ 0·2662
Mean		− 0·2316	− 0·0436	+ 0·1400	+ 0·1756
42 – 82	I	+ 0·6007*	+ 0·0184	− 0·0244	− 0·1300
	II	+ 0·0783	− 0·1380	+ 0·3799	− 0·0881
	III	− 0·0792	− 0·2428	+ 0·2305	− 0·1509
	IV	+ 0·0156	− 0·3786	− 0·1487	− 0·2676
Mean		+ 0·1538	− 0·1852	+ 0·1093	− 0·1591

With one exception, marked *, ($P = 0{\cdot}01$), none of the coefficients is significant. The only trend is that of the mean coefficients in each cruise in stations 1– 41, in which they gradually change from negative to positive. The evidence from this table may be summarized as follows: sharp aggregation of pilchards on size group I did take place on Cruise VII in the Western Channel and there was a slight tendency to aggregate on any size group later in the Eastern Channel.

When correlation between the zooplankton and the pilchard eggs was estimated for the Western Channel, a slightly different result was obtained as shown in Table XI.

No coefficient is significant, but all are positive and in general higher than those on echo traces. Hence, it appears that the spawning (and pre-spawning fish) may aggregate to some degree upon zooplankton patches. Consequently the echo traces must include fish that do not make such an aggregation. It is thought that such fish are spent pilchards but, of course,

Table XI: *Correlation coefficients between numbers of Stage I pilchard eggs and total zooplankton/m³*

Cruise	*VII*	*VIII*	*X*
Stations 42 – 82	+ 0·1190	+ 0·2886	+ 0·2418
n	26	37	35

the echo traces may also include other pelagic fish. However, when the phytoplankton correlations are also considered, the differences between coefficients on echo traces and on numbers of eggs are attributed to a separation into spawning and spent fish, and the significant correlation between echo traces and algal volumes are thought to be an effect of an earlier aggregation of spawning fish on zooplankton. Hence it is probably true that the spawning fish aggregate on zooplankton as shown by Table XI and that the spent fish do not, which explains the results given in Table X, because there is no distinction between spent and spawning fish in echo trace counts.

From the evidence of the distribution of echo traces, it is likely that some eastward movements of the fish took place during April, May and June. As no feeding aggregation took place as sharply as that of the herring on *Calanus*, it may be because the fish are spawning as they feed. Now, as the spawning tended to move eastwards (within the Western Channel anyway), it is possible that the fish actively migrate eastward searching for food. Fish aggregate sharply on the food patches off Start Point in April as shown and these fish subsequently spawn; no further feeding aggregation is observed in the Western Channel, because spawning aggregations become prominent, as shown in Fig. 5. In the Eastern Channel, feeding aggregations may assert themselves because of the relative lack of spawning. It is possible that three events took place in the following order, firstly that the nearly ripe fish aggregated sharply on to some food patches, completing their over-winter trend towards maturity and, secondly that spawning started after this aggregation, and, thirdly that the fish moved in to the Eastern Channel and formed feeding aggregations; whether the latter are spent or not we do not know. Thus, the concentration of pilchards in the centre of the Western Channel, and the patchiness of the egg distributions are effects of feeding and spawning. Fish do move up Channel and do spawn there, and even spawn far into the North Sea, but this is probably only a movement by a small part of the population.

A little more information may be obtained by comparing the distributions of eggs, echo traces and zooplankton organisms. Before we do this, however, we must describe the distributions of zooplankton, which are shown in Fig. 12. There are four groups of copepods, *Calanus*, *Pseudocalanus*, *Temora* and *Centropages;* other species are included as follows:

I	*Calanus finmarchicus*	*Candacia armata* *Metridia lucens* *Corycaeus anglicus* *Oithona spp* *Isias clavipes*
II	*Pseudocalanus elongatus*	*Paracalanus parvus*
III	*Temora longicornis*	*Acartia clausi* *Parapontella brevicornis*
IV	*Centropages typicus* and exclusive.	*Centropages hamatus*, which are mutually

Fig. 12(a) shows the distribution of stages of *Calanus*. On Cruise VII there are two groups, Stages I and II near Start Point and Stages III, IV, V extending southward into mid-Channel. On Cruise VIII there is a group of Stages I, II and III in mid-Channel south of Start Point. If the older stages each took about ten days to develop, it is possible

(a) (b) (c) (d)

Fig. 12. *Distribution of Zooplankton as n/m²* on Cruises *VII, VIII, X and XII*, Sir Lancelot, 1950.

(a) *Calanus* copepodite stages I–V
(b) *Pseudocalanus* and *Paracalanus*
(c) *Temora* and *Acartia*
(d) *Centropages typicus* and *Centropages hamatus*

that the group in mid-Channel on Cruise VIII is descended from the group in mid-Channel on Cruise VII. Comparing Cruises VIII and X, there are again two groups, one in mid-Channel South of Start Point and one in the extreme West; as there is no marked difference in the distribution of stages, it might be concluded that the rate of development had speeded up to perhaps five to eight days per stage, as there was a month's interval between each cruise. The mid-Channel patch is still in position on Cruise XII, but nothing can be said about the western patch because the two western-most lines of the grid were not completed on that cruise.

It appears that from April to July a *Calanus* patch off Start Point gradually moved southwards; at the same time another patch moved in to the area from the south-west to the region just west of Start Point. The implication is that the Channel waters as a whole were comparatively static and that there was some southerly movement in the west. The patches of *Pseudocalanus* and *Paracalanus* in the Western Channel followed very roughly the same slow path as did the *Calanus* patches (Fig. 12b); there was apparently very little eastward movement. Again examining the patches of *Temora* and *Acartia* in all cruises (Fig. 12c) it is shown that there were three major patches—off the Channel Islands, in the Baie de la Seine and in the Straits of Dover.

It is of course possible that the simple interpretation reached above is misleading because the animals grow and die and reproduce and bear no necessary relation to the drift of a water mass. However, the contour levels were drawn at the highest significant levels by the method described in Cushing (1953) and so a contour at 30,000 beneath m^2 on Cruise X is roughly comparable with one drawn at 10,000 beneath m^2 on Cruise VIII. The size of patches are certainly not comparable between cruises, using this rough and ready method, but it is probable that their positions, as in larger areas of the Channel, are roughly correct.

Some confirmation for the static state of plankton patches in the Channel may be derived from the distributions of *Centropages typicus* and *Centropages hamatus* (Fig. 12d). These extraordinary and exclusive distributions occur in all four cruises, contoured at the same level of numbers for each species on any cruise, although that level is different from cruise to cruise. The sharp boundary between the two distributions runs from the Isle of Wight or Portland across to the North coast of Brittany; the fact that it remains in the same position throughout the four cruises reinforces the view that the plankton patches were static during this period. A rough generalization may be made that *Calanus* lives in the region occupied by *Centropages typicus* and that *Temora* lives in the region occupied by *Centropages hamatus; Pseudocalanus* lives in both regions.

The use of correlation coefficients between distributions of plankton and soundings on fish did not reveal the causes of the pilchard distributions very clearly. Comparison of the charts of echo surveys, pilchard eggs and plankton yields the following conclusions. On Cruise VII echo traces and eggs appear with *Calanus* and *Pseudocalanus* off Start Point. On Cruise VIII, traces and eggs appear in general in the centre of the Western Channel, where *Calanus* and *Pseudocalanus* are concentrated. On Cruise X, traces are found all over the Channel, but eggs are in the main limited to the west. On Cruise XII, both eggs and echo traces are discontinuously distributed, related if anything to the distribution of *Temora*.

The examination of the zooplankton distributions lead to the following tentative conclusions:

(a) patches of plankton animals remain roughly in the same position from April to July, but fish move eastward;

(b) a sharp aggregation can occur in spring when fish appear from the Wolf Rock moving eastward. The fish probably feed on *Calanus* or *Pseudocalanus*, and with them drift southward from Start Point;

(c) aggregations of fish, after the first stage, are possibly spawning aggregations. There is no well-defined spawning ground unless it be all the Western Channel; sharp patches of pilchard eggs are found here and there, e.g., off the north coast of Brittany and on the edge of the Thames estuary;

(d) when the fish are spent, they probably start feeding again during the late summer.

6. Variations in Abundance of Pilchards

The English catch of pilchards (about 3,000 to 5,000 tons/yr) appears to be a very small proportion of the stock (which is probably about 800,000 tons wet weight). Hence variations in the annual catch could be quite independent of variations in abundance. Some evidence of variation in abundance may be obtained from four sources, the young fish catches made at International Station E.1 since 1924, the annual catches since 1886, the exports to Italy since 1771 and the presence or absence of a pilchard fishery in Irish waters since the seventeenth century.

The average numbers of clupeid larvae caught off the Eddystone with a ring trawl have been recorded by Russell (1931, 1935 *et. seq.*). They were not identified, but it is not unreasonable to assume that those caught in May, June and July are predominantly pilchards; there are almost certainly no herring larvae in high summer in the Western Channel small enough to be caught in a ring trawl, but there is a proportion of sprat larvae, particularly in May. Indeed Clark (1914) and Allen (1916) identified clupeid larvae caught inshore between May and July from 1906–09 and in 1913 as sprats. Of hauls taken at the Eddystone, Russell writes (1935, p. 156): " . . . it is likely, therefore, that any clupeid occurring after the increase of sprat in February, March and April will be pilchard right up to the end of the year when young herring begin to appear in December."

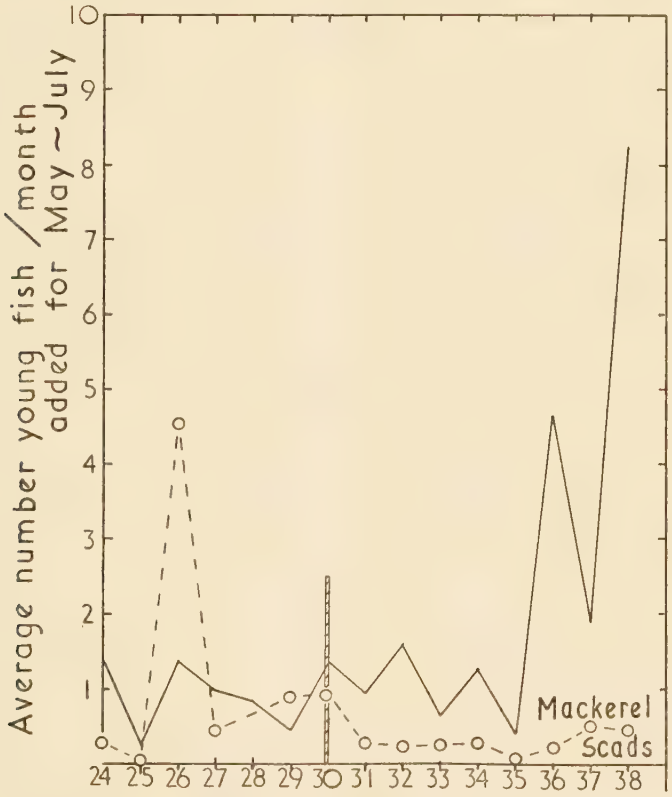

Fig. 13. *The number of young clupeids caught at E.1 from May to July from* 1924–1938. *The pecked line is the sum of mackerel and horse mackerel ('scads')*

Fig. 13 shows the totals of average monthly catches of clupeids in May, June and July from 1924–38. There is a sharp increase in the number of larvae in the summer of 1936 and Mr. Russell has told me that pilchard eggs first became abundant off the Eddystone in the summer of 1935. In the autumn of 1930, 'elegans' water was replaced by 'setosa' water (Russell, 1935) at E.1 and the numbers of summer jellyfish were reduced by four to five times (Russell, 1938, Table II). The changeover from 'elegans' to 'setosa' water started

Sennen Cove and St. Ives; there are violent fluctuations in the west coast landings, probably because they were more dependent on shore seine catches, for which fairly large shoals were necessary. There is a sharp decline of west coast catches after 1905 until the shore seine disappeared during the first world war. On the south coast, there are fluctuations that are obviously due to the wars of 1914–18 and 1939–45, and also to the economic crisis of 1931. Apart from these fluctuations, however, the landings remain at a steady level of about 70,000–90,000 cwt/yr; during the whole period, this level was only exceeded between 1904 and 1906 when it reached 140,000–160,000 cwt/yr. It is possible that this increase was due to a real increase in abundance.

Italian exports are probably reliable until 1913, after which the Italian market for cured pilchards closed and never fully recovered; after 1913, the Italian exports decline in proportion to the total catch landed. If we say that the average exports to Italy lay between 60,000–80,000 cwt/yr between about 1800 and 1913, levels of over 100,000 cwt were reached in 1831–5, 1845–51, 1871–3 and in 1905–6 as shown in Fig. 15. This confirms the conclusion from the annual landings shown in Fig. 14, at the only time during which the two sets of figures overlap.

A study of the history of the Irish pilchard fishery has been made by Went (1946). No quantitative data are recorded, but the presence or absence of pilchards on the Irish coast may be estimated. By going through his records from 1760 and noting those years when 'failure' was recorded, the following results were obtained. There were three periods of abundance found, 1823–43, 1860–85 and 1935 onwards. These correspond very roughly with the periods given by the Italian exports. They do not show expansion in 1906, but they do show a period of abundance starting in 1935, which corresponds to the period noticed by the Plymouth workers.

V. DISCUSSION

In order to clarify the two questions of what region is inhabited by the virtually unfished population of pilchards and to what extent variations in abundance can really be detected, some hypothesis on the migration of the fish is desirable.

Mackerel fishermen from Lowestoft have often reported dense echo traces between the Wolf Rock and the area of the fishery, 50–100 miles to the westward in March and April. During the same fishery, pilchards have frequently been caught in the large-meshed mackerel nets. Towards the end of March, the fish assemble off the Wolf Rock as shown by an echo survey made by *R. V. Platessa* in March 1955 (private communication, G. C. Bolster). By mid-April, the fish move up Channel towards Start Point.

From the end of March to the beginning of May, the fish as recorded on the echo sounder are fairly abundant in the Western Channel, probably locally aggregated on to patches of zooplankton, to feed. This initial feeding probably consummates the over-winter trend towards maturity and the fish spawn, after which they drift and make no active aggregation. Spawning, however, lasts all summer, although the peak of spawning is reached in June. Feeding aggregation probably takes place by fish that have not yet spawned; the spent fish may remain in the water mass in which they spawned, from which the zooplankton has been grazed, which has been abandoned by the feeding ripening fish and in which phytoplankton is free to grow. Some spent fish drift eastwards, forming tenuous food aggregations; other spent fish remain in the west.

In July and August, the echo traces disappear and pilchards are found in the Southern North Sea. The disappearance of echo traces can be attributed to any of three causes: (1) dispersion of the shoals, (2) sinking to the bottom, (3) movement out of the area. The two latter causes should be detected on the echo sounder and as they were not, it seems that the shoals had dispersed. Dispersion to a density not detectable by the echo sounder is quite possible. Hence, it seems unlikely that the disappearance of echo traces in the Channel means that the fish have moved into the Southern North Sea; from the egg

distributions it is probable that most of the fish remain in the Western Channel and that the movement into the North Sea is the movement of a minority.

In the late summer and autumn pilchards gather in Cornish waters, presumably from the Western Channel, for this movement occurs in August in some years. Pilchards also appear in the autumn in the East Anglian herring fishery, in the herring fishery in the Straits of Dover, as célans off Boulogne and in the trammel nets in Rye Bay.

Lastly, the pilchards must gather to the westward in the deep water in mid-winter, for they leave the Cornish waters in December and appear off the Wolf Rock in March.

A migration hypothesis of this type is of little consequence unless it can be related to the hydrographic structure. There appear to be three phenomena which can be linked into the hypothesis of pilchard migration. The first is the sharp division between the distributions of *Centropages typicus* and *Centropages hamatus* which coincides with three features: (a) a line dividing the presence from the absence of a thermocline in summer in the Channel (Dietrich, 1951), (b) the line of equivalent tidal stream speed at 2·5 sea miles/hr (which is the maximum speed at spring tide) (Hansen, 1950), (c) the region of coarse sand which lies eastward of Hansen's line (Pratje, 1950). Consequently, *Centropages typicus*, living to the westward of the line, lives in a region of weakish tides, an occasional summer thermocline and small particles on the bottom, whereas *Centropages hamatus*, in the east, lives in a region of strong tides, no thermocline and large particles on the bottom. The division between the two regions hydrographically is that in the western region, the tidal streams are less rapid and hence there is less turbulence.

The difference between the two tidal regions may be detected in the plankton distributions. It is possible to distinguish in the *Calanus* populations (and presumably *Pseudocalanus* in the west), a movement in the south and west in April, May and June as if they were confined to the western region. The other populations, *Temora*, *Acartia*, which live in the regions of strong tides, tend to remain static. There is some reason for believing that the greater part of the population remains in the western region. It is probable that the fish follow the zooplankton patches before they spawn and that they passively drift after they have spawned, and that when they recover they follow the patches again; hence the fish tend always to follow the drift of the water masses during the summer, which in the Western Channel would be roughly in a clockwise swirl, reversing its direction in autumn to bring the fish back to Cornwall in October (Dietrich, 1950).

VI. SUMMARY

THE English Channel was surveyed for pilchard eggs, echo traces, plankton and temperature in April, May, June, July and August, 1950.

From counts of pilchard eggs an estimate was made of the number of adult pilchards in the area: 10^{10}.

With the use of this figure an estimate was made of the number of fish contributing to each transmission in an echo trace.

A vertical migration of echo traces was observed. No correlation was observed between algal volumes and numbers of pilchard eggs but a correlation was found between algal volumes and the number of soundings on fish. Correlations between zooplankton numbers and pilchard eggs were higher than those between zooplankton numbers and numbers of soundings on fish. It appeared that the maturing fish aggregated on zooplankton patches and that spawning took place there; spent fish drifted in regions of grazed zooplankton and phytoplankton outburst.

It is possible that the present abundance of pilchards was initiated in the 1930/1 biological change observed at E.1 off Plymouth. Landing statistics, Italian exports and evidences of abundance in Ireland have been presented to show some periods of abundance very roughly.

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